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Resource Partitioning by Reef Corals as Determined from Stable Isotope Composition II. $\delta^{15}N$ of Zooxanthellae and Animal Tissue versus Depth[1]

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ABSTRACT: The pattern of resource partitioning versus depth for corals collected in February, 1983, from Jamaica was investigated by analyzing their stable nitrogen isotope composition. Observations were made on isolated zooxanthellae and corresponding algae-free animal tissue from nine species of symbiotic corals at four depths over a 50-m bathymetric range, and from a nonsymbiotic coral at 1 m. $\delta^{15}N$ values versus depth ranged from +3.54 to −2.15 ‰ for zooxanthellae and from +4.71 to +0.23 ‰ for animal tissue. In those species that occurred over a 30- to 50-m depth range, both animal tissue and zooxanthellae tended to be depleted in ^{15}N as depth increased to 30 m. In a few species animal tissue was enriched in ^{15}N from 30 to 50 m. Depletion of ^{15}N in zooxanthellae with increasing depth may be the result of depth-dependent differences in their nitrogen-specific growth rates. Animal tissue was consistently more depleted in ^{15}N than for the nonsymbiotic coral *Tubastrea coccinea* (Ellis) at the same depth, but it was still slightly more enriched in ^{15}N than corresponding zooxanthellae in 16 of 25 paired samples. The latter trend was not correlated with depth. A comparison of $\delta^{13}C$ and $\delta^{15}N$ for zooxanthellae and animal tissue over 50 m revealed a tendency toward depletion of heavy isotopes as depth increases. Increased carbon fixation appears to be accompanied by decreased nitrogen fractionation.

RESOURCE UTILIZATION by scleractinian reef corals is profoundly affected by endosymbiotic dinoflagellates (zooxanthellae). Although coral polyps feed on particulate organic carbon and nitrogen (Lewis and Price 1975, Lewis 1976, 1977, Clayton and Lasker 1982), their phototrophic endosymbionts take up and assimilate inorganic carbon (Muscatine and Cernichiari 1969, Schmitz and Kremer 1977, Crossland et al. 1980, Black and Burris 1983) and nitrogen (Franzisket 1974, Crossland and Barnes 1977, D'Elia and Webb 1977, Muscatine and D'Elia 1978, Webb and Wiebe 1978, Muscatine et al. 1979, Muscatine 1980*a*, Burris 1983, D'Elia et al. 1983, Wafar et al. 1985, Summons et al. 1986, Anderson and Burris 1987, Rahav et al. 1989) from the environment and from host catabolism. Organic carbon and nitrogen is translocated from algae to host (Muscatine 1980*b*, Falkowski et al. 1984) and possibly from host to algae (e.g., see Cook 1983, Steen 1986). The symbiotic algae also enable the retention and recycling of carbon and nitrogen atoms within the coral. These features confer an apparent selective advantage on coral animals in oligotrophic environments. There is little information, however, on how depth and light attenuation might influence these potential fluxes and consequently the selective advantage of the symbiosis to the partners.

In previous studies, Davies (1984), McCloskey and Muscatine (1984), and Muscatine et al. (1984) noted that photosynthetic rates by zooxanthellae in shallow-water corals are high and that carbon translocated from algae could meet the daily carbon demand of the animal for respiration and

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growth. In contrast, in deep-water corals, photosynthetic rates are low and much less photosynthetically fixed and translocated carbon is available for animal respiration and growth. McCloskey and Muscatine (1984) predicted that in deep water, reduced input of photosynthetically fixed and translocated carbon may be supplemented by input of carbon from allochthonous sources. Muscatine et al. (1989) attempted to evaluate this prediction by analyzing the stable carbon isotopes of coral animal tissue and zooxanthellae as a function of depth. Their data revealed that $\delta^{13}C$ of zooxanthellae was relatively high in shallow water. These high values were interpreted as the result of diffusion-depletion of internal CO_2 at high rates of photosynthesis and consequent minimal stable isotope discrimination (see also Goreau 1977). Zooxanthellae $\delta^{13}C$ became lower as depth increased and as light for photosynthesis diminished. Animal tissue $\delta^{13}C$ was slightly lower than zooxanthellae $\delta^{13}C$ in shallow water, probably as a result of translocation of photosynthetically fixed carbon from zooxanthellae to animal. As depth increased, the animal tissue exhibited a disproportionately lower $\delta^{13}C$, suggesting that more particulate organic carbon (POC) is taken up in deep water or that at the lower rates of photosynthesis CO_2 was no longer limiting.

To gain further insight into resource utilization by reef corals, we examined the $\delta^{15}N$ of zooxanthellae and animal tissue versus depth in the same coral samples as those analyzed by Muscatine et al. (1989). $\delta^{15}N$ values for marine organisms generally range from about -3 ‰ to about $+20$ ‰ (Owens 1987), but some organisms from hydrothermal vents or hydrocarbon seeps, or possessing endosymbiotic bacteria, exhibit values as low as -12.9 ‰ (Rau 1981, Paull et al. 1985, Brooks et al. 1987, Conway et al. 1989). $\delta^{15}N$ values reflect the nature of the source nitrogen, which may undergo only minimal fractionation when it is limiting (Wada and Hattori 1976, Owens 1987) or when atmospheric nitrogen is fixed by marine cyanobacteria (see references in Macko et al. 1984). Alternatively, source nitrogen may undergo maximal fractionation during assimilation (Wada and Hattori 1978, Minegawa and Wada 1980, Wada 1980, Macko et al. 1986, 1987). $\delta^{15}N$ values are also useful as indicators of trophic level (Van Dover and Fry 1989).

The data presented here show that both the zooxanthellae and the animal tissues in Jamaican scleractinian corals tend to be depleted in ^{15}N, particularly as depth increases. Depth-dependent variables that may contribute to ^{15}N depletion are discussed.

MATERIALS AND METHODS

Methods for sampling corals, separation of zooxanthellae and animal tissue, and analytical techniques were described by Muscatine et al. (1989). Briefly, 10 species of corals (nine symbiotic, one nonsymbiotic) were collected from 1 and 10 m depth from the back reef and from 10, 30, and 50 m depth from the fore-reef at Discovery Bay, Jamaica, in February 1983. Tissue was removed from whole colonies or from large pieces of massive corals to minimize sample heterogeneity within colonies. Algae and animal tissues were separated by a series of careful centrifugations and washings. Algae were recovered as pellets, and animal tissue was deposited on precombusted glass fiber filters (Reeve Angel). Both fractions were dried at 50°C. Samples were combusted as described by Minegawa et al. (1984). Mass spectrometry was performed on a Varian MAT 250 instrument. The $^{15}N/^{14}N$ of the samples is reported as $\delta^{15}N$, in units per mil (‰), where:

$$\delta^{15}N\ (‰) = [(R_{sample}/R_{standard}) - 1] \times 1000$$

and

$$R = {}^{15}N/{}^{14}N$$

Atmospheric nitrogen was the standard. The analytical precision of these measurements was 0.2 ‰.

RESULTS

The values of $\delta^{15}N$ for each species versus depth ranged from $+3.54$ to -2.15 ‰ for

TABLE 1

$\delta^{15}N$ FOR ALGAE AND ANIMAL TISSUE FROM JAMAICAN CORALS OVER A 50-m BATHYMETRIC RANGE

CORALS	DEPTH			
	1 m	10 m	30 m	50 m
Symbiotic corals				
Madracis mirabilis (Duchassaing & Michelotti)				
Algae	+3.54	+3.26	+2.64	*
Animal	+3.90	+3.05	+1.84	*
Acropora cervicornis (Lamarck)				
Algae	+1.76	+1.68	+0.16	*
Animal	+4.11	+1.86	+1.56	*
Agaricia agaricities (Linnaeus)				
Algae	+1.64	+1.85	+1.86	+0.30
Animal	+3.02	**	+1.48	+1.54
Acropora palmata (Lamarck)				
Algae	+1.76	+1.48	*	*
Animal	**	+2.13	*	*
Porites astreoides Lamarck				
Algae	+2.99	+2.30	+1.74	*
Animal	+2.79	+2.10	+2.04	*
Montastrea annularis (Ellis & Solander)				
Algae	+3.00	+1.83	+2.21	−0.16
Animal	+3.32	+2.41	+0.23	+1.87
Montastrea cavernosa (Linnaeus)				
Algae	+0.95	+0.35	−2.15	−1.73
Animal	+2.96	+1.11	+1.16	+3.43
Eusmilia fastigiata (Pallas)				
Algae	+3.45	+2.18	+0.94	*
Animal	+3.45	+2.52	+2.76	*
Dendrogyra cylindrus Ehrenberg				
Algae	*	+2.43	*	*
Animal	*	+2.23	*	*
Nonsymbiotic coral				
Tubastrea coccinea (Ellis)	+4.74	*	*	*

*, not found at depth; **, samples lost.

algae and from +4.11 to +0.23 ‰ for animal tissue (Table 1). In those species that occurred over a 30- to 50-m depth range, both zooxanthellae and animal tissue tended to be depleted in ^{15}N as depth increased, although in *Montastrea annularis* (Ellis & Solander) and *M. cavernosa* (Linnaeus) at 50 m, animal tissue was again enriched in ^{15}N.

There were differences between $\delta^{15}N_{animal}$ and $\delta^{15}N_{algae}$ in each species. Animal tissue was more enriched in ^{15}N than algae in 16 of the 25 paired samples (mean ± SD = 1.51 ± 1.3 ‰; range, 0.30–5.16 ‰). In the remaining nine, the $\delta^{15}N$ animal values were equal to or lower than those of corresponding algae (mean ± SD = 0.46 ± 0.61 ‰; range, 0.18–1.98 ‰).

The $\delta^{15}N$ value for *Tubastrea coccinea* (Ellis) is +4.74 ‰ and is taken as representative of coral animal tissue at 1 m that has acquired particulate and/or dissolved organic nitrogen in the absence of a photosynthetic endosymbiont.

DISCUSSION

$\delta^{15}N$ *of Zooxanthellae*

$\delta^{15}N$ values for zooxanthellae in Jamaican corals range from −2.15 to +3.54 ‰. The data cluster at the low end of the range of values representative of marine organisms. Interpretation of the absolute values of $\delta^{15}N$

for the algae and animal must await data on the $\delta^{15}N$ values of the source nitrogen, which, at present, are unknown. The most important sources of dissolved inorganic nitrogen (DIN) for symbiotic dinoflagellates seem to be nitrate and ammonium from seawater and ammonium from coral animal catabolism (D'Elia 1988, Rahav et al. 1989). Other potential sources include nitrate and ammonium from local sources such as groundwater (D'Elia et al. 1981), nitrification associated with bacteria in sponges (Corredor et al. 1988) and coral skeletons (Szmant-Froelich and Pilson 1977, Wafar et al. 1985), coral head porewater (Risk and Muller 1983), and migrating fishes (see, for example, Meyer and Schultz 1985*a*,*b*).

An interpretation of the trend in depletion of zooxanthellae ^{15}N with depth is suggested by observations of Wada and Hattori (1978; see also Minegawa and Wada 1980) on cultured marine diatoms. They demonstrated that isotope fractionation of nitrate and ammonium was negligible during uptake, but substantial during assimilation, and that fractionation was inversely proportional to growth rate. The highest fractionation occurred when growth was light-limited and N-sufficient. Because the specific growth rate of zooxanthellae in at least one coral species tends to be higher in high-light habitats than in shade (Muscatine et al. 1989), the depth profile for zooxanthellae $\delta^{15}N$ could be interpreted on the basis of relative specific growth rates of light-sufficient, nutrient-limited zooxanthellae in shallow water and light-limited, nutrient-sufficient zooxanthellae in deep water. A few observations support this scenario.

Zooxanthellae in corals are very effective scavengers of nitrogen, often taking up ambient DIN at or below concentrations of 1 μM and effectively retaining host catabolic ammonium so that, under normal conditions, little host catabolic ammonium is released to the environment (Muscatine and D'Elia 1978, Cook and D'Elia 1987, Cook et al. 1988, Rahav et al. 1989, Stambler et al. 1991). However, there is a growing body of evidence that suggests that growth rate or biomass increase of zooxanthellae in shallow-water corals and other symbiotic cnidarians may be nitrogen-limited (Cook and D'Elia 1987, Cook et al. 1988, Dubinsky et al. 1989, Høegh-Guldberg and Smith 1989, Muscatine et al. 1989). N-limited cells in shallow water might assimilate most of the available DIN and consequently might exhibit minimal stable isotope fractionation (Wada and Hattori 1976). In contrast, zooxanthellae in light-limited deep-water corals may grow more slowly and consequently exhibit greater isotope discrimination. Wilkerson et al. (1988) estimated generation times for zooxanthellae from the same set of corals as analyzed in this study. When our $\delta^{15}N$ data are plotted against their growth rate data (as generation times) for zooxanthellae from all species at all depths, no significant correlation emerges ($\delta^{15}N = 1.38 + 0.02$ (generation time) ($n = 26$; $r = 0.01$). This appears to argue against a "growth rate fractionation" hypothesis. However, generation time is derived from zooxanthellae mitotic index and is a function of the standing stock of cells. It does not take into account the translocated nitrogen that does not appear in the standing stock of cell nitrogen. Consequently, the parameter of interest is the nitrogen-specific growth rate (u_N), manifested by the uptake and assimilation of DIN by zooxanthellae and the translocation of dissolved organic nitrogen (DON) to the host. That is, in symbiotic algae, and perhaps even in some free-living algae (see Zehr et al. 1988), nutrient uptake and assimilation is uncoupled from cell growth at the low specific growth rates exhibited by zooxanthellae in hospice. For example, from data on uptake rates of ^{15}N (as ammonium) by the shallow-water Red Sea coral *Stylophora pistillata* Esper, Muscatine et al. (1984) estimated that u_N was 0.31 day^{-1} for light-adapted cells and 0.25 day^{-1} for shade-adapted cells, a 20% decrease. This trend is consistent with our conjecture that u_N for coral zooxanthellae may decrease with decreasing irradiance at greater depths, so that rates of uptake, assimilation, and translocation are lower and the scope for fractionation is higher.

Alternatively, the lower $\delta^{15}N$ values (< 1.00 ‰), especially as depth increases, are

close to the generally accepted value of 0.00 ‰ for dissolved nitrogen in seawater (Owens 1987) and so could be derived from acquisition of DIN from fixed nitrogen sources. The lower values could also result from assimilation of local sources of ^{15}N-depleted ammonium, such as host catabolism, zooplankton excretion (Checkley and Entzeroth 1985), or from greater discrimination by the algae of locally elevated concentrations of ammonium and nitrate.

δ^{15}N *of Animal Tissue*

δ^{15}N of animal tissue ranged from +4.71 to +0.23 ‰. Corals living at 1 m depth had consistently lower animal tissue δ^{15}N values (mean ± SD = 3.36 ± 0.49 ‰; range, 2.79–4.11 ‰) than the nonsymbiotic coral *Tubastrea coccinea* (+4.74 ‰), living at the same depth. The reasons for these differences are still obscure, but are undoubtedly related to the fact that the diet of *T. coccinea* is solely allochthonous particulate and DON enriched in ^{15}N (e.g., zooplankton), whereas the diet of the symbiotic corals also includes substrates acquired from the zooxanthellae. Allochthonous substrates may also account for the increase in animal tissue δ^{15}N in *M. annularis* and *M. cavernosa* at 50 m depth. This interpretation is consistent with the previous interpretation that δ^{13}C of animal tissue versus depth is influenced by allochthonous POC (Muscatine et al. 1989).

Although the δ^{15}N values for animal tissue are low relative to those for *T. coccinea*, in the majority of coral species they are still slightly higher than those of their corresponding zooxanthellae. The difference, although not correlated with depth, is consistent with the general observation that, in most cases, the δ^{15}N of marine invertebrates and vertebrates is greater than their dietary δ^{15}N by an average of 2.6 ± 2.1 ‰ (Owens 1987). Coral animal cells could acquire ^{15}N-enriched substrates by translocation from zooxanthellae. Coral zooxanthellae release alanine in vitro (Muscatine and Cernichiari 1969) and may do so in situ (Lewis and Smith 1971). In addition, some zooxanthellae secrete nitrogen-containing macromolecules that may be acquired by the host (Markell and Trench 1993). Animal tissue could also be enriched in ^{15}N relative to zooxanthellae as a result of protein catabolism and excretion of isotopically light ammonium. More than 90% of the ammonium excreted by *Stylophora pistillata* is taken up by resident zooxanthellae (Rahav et al. 1989). Retention of such host excretory ammonium by zooxanthellae may be a general phenomenon among corals (Muscatine and D'Elia 1978) and would exacerbate the tendency of zooxanthellae to be depleted in ^{15}N relative to animal tissue.

Comparison with Other Endosymbioses

Relatively low (i.e., negative) δ^{15}N values have been reported for some, though not all, endosymbioses involving bacteria in worms and clams from communities associated with hydrothermal vents and deep seeps (Rau 1981, Paull et al. 1985, Brooks et al. 1987, Van Dover and Fry 1989, Rau et al. 1990*a*). The low δ^{15}N values are attributed to either assimilation of isotopically depleted nitrogen sources, fractionation, or nitrogen fixation (Rau 1985). Bacteria and host tissues in protobranch bivalves (*Solemya reidi*) from shallow-water reducing sediments have similar δ^{15}N values. The similarity is attributed to assimilation by bacteria of a nonlimiting DIN source, such as porewater ammonium, and translocation of DON to the host (Conway et al. 1989). However, like endosymbiotic algae, although the cell-specific growth rate of endosymbiotic chemoautotrophic bacteria in *S. reidi* is relatively low (see Cavanaugh 1985), the nitrogen-specific growth rate could be relatively high and as such could be a factor that influences δ^{15}N values.

δ^{13}C *and* δ^{15}N *versus Depth*

The analysis of multiple stable isotopes has been used to provide insight into the diet of a variety of organisms and their trophodynamics (see Owens 1987, Rau et al. 1990*a*,*b*, 1991). Figure 1 provides a first glimpse of variation in δ^{13}C and δ^{15}N versus depth for animal tissue and zooxanthellae in Jamaican

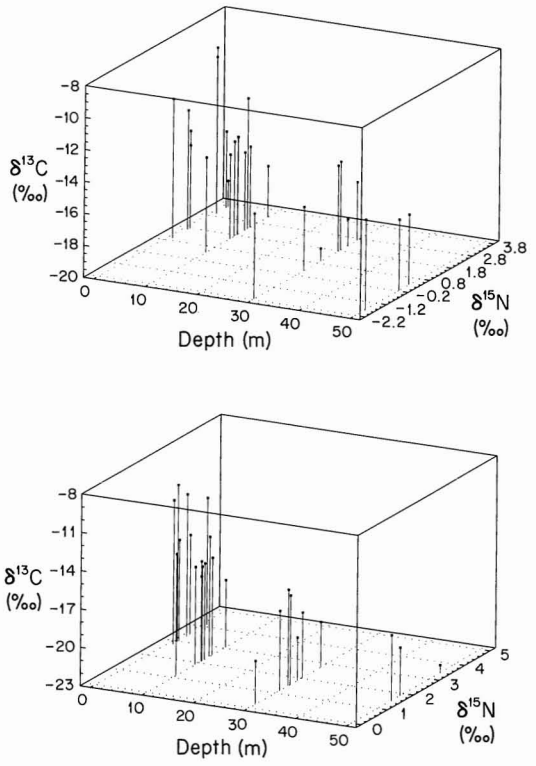

FIGURE 1. $\delta^{15}N$ and $\delta^{13}C$ for zooxanthellae (upper) and animal tissue (lower) versus depth for nine species of Jamaican corals. Data from Table 1 (this paper) and Table 1 of Muscatine et al. (1989).

corals over a 50-m bathymetric range. The data reveal a tendency toward depletion of ^{13}C and ^{15}N in both the zooxanthellae and animal tissue in most species as depth increases. Increased carbon fixation is apparently accompanied by decreased N fractionation. Additional measurements may prove useful in interpreting stable isotope abundances and in elucidating resource partitioning strategies in symbiotic corals.

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